

# INVERTEBRATES ASSOCIATED WITH COARSE WOODY DEBRIS IN STREAMS, UPLAND FORESTS, AND WETLANDS: A REVIEW

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**Abstract.** We reviewed literature on the invertebrate groups associated with coarse woody **debris** in forests, streams, and wetlands, and contrasted patterns of invertebrate community development and wood decomposition among these ecosystems.

## INTRODUCTION

Coarse woody debris (**CWD**) is defined as logs, snags, and chunks of dead wood greater than 2.5 cm diameter (Harmon et al., 1986). This material supports a diverse invertebrate **fauna** and is an important source of energy for many ecosystems (Triska and Cromack, 1980; Harmon et al., 1986). The sink of carbon and nutrients in CWD becomes available through **fragmentation** and decomposition, which is facilitated by the invertebrates that colonize and exploit it (Swift, 1977).

## INVERTEBRATE-CWD INTERACTIONS

CWD in streams provides invertebrates with **food**, **refugia from flood** disturbance and predation, and sites for resting, oviposition, pupation and emergence (Benke et al., 1984; Everett and Ruiz, 1993; Hax and Golladay, 1998). Especially in streams and rivers with sand or silt substrates, high densities of stream macroinvertebrates are associated with CWD (Benke et al., 1984; Smock et al., 1985; Benke, 1998). Some of the **stream** invertebrates associated with wood are xylophagous (gougers, *borers*, and shredders) while most others **feed** on detritus, biofilms, and prey that accumulate on CWD (collector-gatherers, scrapers, and predators) or simply use **wood** as habitat (collector-filterers) (Wallace and Webster, 1996).

When CWD enters **streams**, Cbironomidae **larvae** are the first to colonize and they remain numerically dominant thereafter (Nilsen and Larimore, 1973; Thorp et al., 1985; Hax and Golladay, 1993; Magoulick,

1998). Trichoptera and wood boring **Diptera** also occur early in the colonization cycle. Communities **stabilize** after 6 to 8 wks (Thorp et al., 1985; Hax and Golladay, 1993; Magoulick, 1998). Various physical **parameters**, such as substrate type, dissolved oxygen (DO) level, current velocity, and **sediment** particle size **affect** colonization and community development on **CWD** (Thorp et al., 1985; Magoulick, 1998). These **early** colonizers make CWD structurally more complex by building cases or boring into the wood (Dudley and Anderson, 1982). Fine particulate organic matter accumulates in and around invertebrate **created** structures and a highly nutritious biofilm develops on CWD **surfaces** providing food for a diversity of other invertebrates (Hax and Golladay, 1993). Invertebrate activity and **fungal** invasion **softens** wood (Dudley and Anderson, 1982; but see Hax and Golladay, 1993). Hydropsychid **caddisfly** larvae can fragment wood through their retreat-building habits (Wallace et al., 1996). **Elm**id gougers form channels in wood and create interstitial spaces that facilitate colonization and exploitation of CWD by other stream invertebrates (McKie and Cranston, 1998). As wood becomes **soft** and **punky** in the late stages of decay, oligochaete and dipteran detritivores become **abundant** (Dudley and Anderson, 1982).

The invertebrates that exploit CWD in upland forests can be grouped as either wood inhabitants or wood invaders (Swift, 1977). Inhabitants are organisms that depend on wood to complete their life cycle and many can attack **living** trees, converting them to CWD (Hanula, 1996). Some spend a **large** portion of their life cycle in dead wood. **Invaders**, on the other hand, can exist in other habitats and do not **rely** solely on wood to complete their life cycles (Harmon et al., 1986; Hanula, 1996).

During the first year following CWD input, **xylophagous** insects **phoretically** disperse fungi, mites, and **nematodes** (Hanula, 1996). The bark begins to loosen and a **subcortical** community of **dipteran** larvae, **mites**, centipedes, and coleopteran predators develops

(Savely, 1939). In 2<sup>nd</sup> year logs, wood rotting fungi become **common** and **soften** the **sapwood**. **Social** insects **such as** carpenter ants **and** termites excavate wood for nest formation (Harmon et al., 1986). Invertebrates present at this stage primarily feed on fungi and rotten **sapwood**. **Rotten-wood borers**, excavators, and a diversity of **dipteran larvae** become established in the subcortical layer. The bark remains **intact but** numerous exit holes exist **from** emergence of adult borers (Savely, 1939; Fager, 1968; Harmon et al., 1986). During the 3<sup>rd</sup> year, bark continues to loosen and the **sapwood** disappears, although **heartwood** remains largely intact. **Fungal** and rotten-wood feeders and predators are dominant. A similar **fauna** persists as the heartwood rots and decomposed wood is incorporated into the forest floor (Savely, 1939; Fager, 1968; Harmon et al., 1986).

In forested wetlands, aquatic and, terrestrial conditions occur. Collector-gatherers and predators dominate the aquatic invertebrate community on wetland CWD (Gladden and Smock, 1990; Golladay et al., 1997; **Braccia** and **Batzer**, unpublished). Shredders, collector-filterers, and scrapers are rare (Thorpe et al., 1985; **Braccia** and Batzer, unpublished). In a **cypress-tupelo** swamp, Thorpe et al. (1985) found that **Chironomidae** were the first to colonize. By 8 **wks**, **oligochaetes** and chironomids became **co-dominant**; **Ephemeroptera**, **Coleoptera**, and Trichoptera occurred, but only in small numbers. Aquatic invertebrate densities on wetland **CWD** can range from 1,000 - 6,000 **individuals/m<sup>2</sup>** of wood surface area (Thorpe et al., 1985; Gladden and Smock, 1990; Golladay et al., 1997), and densities can be influenced by the depth and position of the wood in the water column (probably because of variation in DO levels). Wood extending to the water's **surface** can provide oxygenated habitat for invertebrates when environmental conditions stagnate (Golladay et al., 1997).

In a southeastern beaver pond, **Pickard** and Benke (1998) estimated annual secondary production for the amphipod *Hyalloa azteca* on wood as 434 **AFDM/m<sup>2</sup>/yr**, which was much lower than the 801 **AFDM/m<sup>2</sup>/yr** on nearby benthic substrates. Sediments and leaf litter may be superior habitat to CWD for aquatic invertebrates in some **wetlands** (Gladden and Smock, 1990), but not others (Golladay et al., 1997). During dry periods, CWD can provide valuable **refugia** for aestivating aquatic invertebrates (Wiggins et al., 1980; Batzer et al., 1999). However, many prefer soil to **CWD** (Gladden and Smock, 1990; Batzer et al., 1999).

**When** forested wetlands dry, terrestrial invertebrates

invade the exposed forest floor. This wetland fauna is often overlooked **because** most research focuses solely on aquatic invertebrates. However, diversity of the aquatic **taxa** is dwarfed by the terrestrial fauna (**Batzer** et al., 1999). On a South Carolina **bottomland** hardwood wetland, we have found an abundance of terrestrial **Coleoptera** (**Passalidae**, **Carabidae**, **Staphylinidae**), **Hymenoptera** (**Formicidae**), **Diplopoda**, **Chilopoda**, and **Isoptera** associated with CWD (**Braccia** and Batzer, unpublished data). These invertebrates probably influence wetland CWD in many of the same ways as they do upland forest CWD.

## CWDDECOMPOSITION

In streams, anaerobic conditions created by water logging slow decay (**Triska** and Cromack, 1980). Invertebrate activities, movements of water-borne particles, and microbial activity influence rates of wood decomposition. In a small **headwater** stream, Wallace et al. (in press) estimated an annual decay rate of  $k = 0.0083 \text{ yr}^{-1}$  ( $k$  is the exponential rate of wood decay) for small CWD (which is extremely slow) but warned that this value may actually be an overestimate (Harmon et al., 1986). In the same basin, Webster et al. (ii press) reported that 5 years after CWD input only the surface layer of bark had been removed. Decay of wood itself was not evident until exposed ends of the branches began to deteriorate after 8 years.

Decay rates of CWD in upland forests vary widely (Abbott and Crossley, 1982; Mattson et al., 1987; Stone et al., 1998). **Wood** may decompose in only a few years in the tropics or it may take decades in northern temperate forests. Location and position of the wood within the ecosystem, macro- and microclimate, size, tree species, and invertebrates **affect** CWD decomposition in upland forests (Harmon et al., 1986). For oaks (*Quercus* spp., 25-35 cm dia.), Schowalter et al. (1998) reported  $k = 0.12 \text{ yr}^{-1}$  for the first year and a slower average of  $k = 0.06 \text{ yr}^{-1}$  for the following 4 years. We found only a single decay estimate for wetland CWD. In a seasonally flooded wetland in Illinois, an average  $k = 0.089 \text{ yr}^{-1}$  was calculated for 5-cm dia. silver maple (*Acer saccharinum*) logs (Chueng and Brown, 1995).

## APPLYING PARADIGMS TO WETLANDS

The aquatic invertebrate communities associated with wetland CWD are simple in comparison to streams

(Table 1). The lack of gougers, filterers shredders scrapers, and grazers likely results from the low DO levels, slow water velocities, and periodic drying conditions characteristic of wetlands. Aquatic invertebrates may not be as important to fragmenting CWD in wetlands as in streams. The suspected higher decomposition rates of wood in wetlands probably results from dry season processes.

Terrestrial invertebrate communities on wetland and upland CWD are fairly similar (Table 1). Some upland organisms may not occur in wetlands because they can not withstand long periods of flooding. However, we have found that large numbers of terrestrial invertebrates can persist in flooded wetlands by living above the water's surface (on floating wood or partially submerged stumps). Larger CWD in these systems

retains moisture well into the dry season, and moist wood typically attracts invertebrates (Triska and Cromack, 1980). The favorable conditions for invertebrate, fungal, and microbial decomposers may make CWD decay particularly rapid in dry wetlands. While the aquatic fauna on wetland CWD is clearly important, we suspect that the terrestrial fauna is even more important to overall ecosystem function.

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Table 1. Invertebrates Associated With CWD

	streams	upland forests	wetlands
invertebrate community	borers, collector-filterers, collector-gatherers, gougers, grazers, predators, shredders, scrapers	borers, fungal-and rotten wood-feeders, predators	Aquatic: collector-gatherers, predators Terrestrial: borers, fungal and rotten wood-feeders, predators
invertebrate diversity/abundance	high: for wood in sand and silt low: for wood in cobbles and gravel	high: moist conditions low dry conditions	Aquatic: low diversity, variable abundance Terrestrial: moderate to high?
key abiotic constraints	water velocity, wood condition (state of decay)	moisture, microclimate within wood	Aquatic: DO, drying Terrestrial: flooding other?
wood decomposition	extremely slow	moderate	Aquatic: slow Terrestrial: faster?

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